PROTANDRY IN TWO SPECIES OF STREPTANTHUS (CRUCIFERAE)

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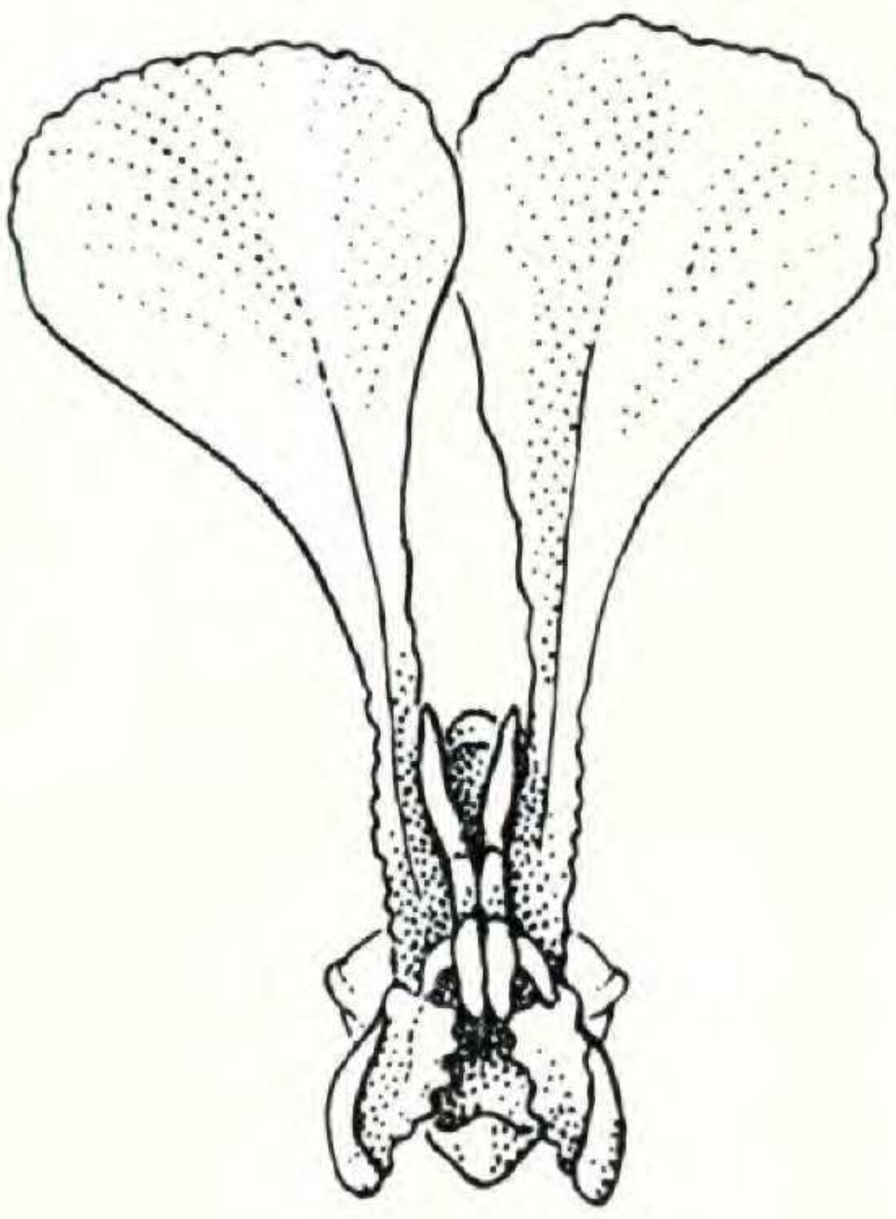
The widespread presence of self-incompatibility as an outbreeding mechanism in the Cruciferae has been emphasized particularly by Bateman (1955a). Of the eleven tribes reported upon, only the *Streptantheae,* in which but a single species of *Caulanthus* had been investigated, showed no self-incompatibility. During the last year, we have had two species of *Streptanthus, S. cutleri* Cory and *S. carinatus* Wright, in greenhouse cultures. These were grown from seed collected in western Texas. Isolation tests on both species show they are not only self-incompatible but that the flowers are protandrous as well. The *Streptantheae* may now be added to the list of tribes showing self-incompatibility.

In his major paper, Bateman (l.c., p. 63) made the statement that there is no protandry, no protogyny and no dioecy in the Cruciferae. A later short note (Bateman, 1955b) acknowledged the presence of dioecy in *Lepidium sisymbroides* Hook. as an exception to the rule. Now, we bring to the attention of botanists an exception to the generally accepted idea that there is no protandry in the Cruciferae. At the same time, one of the most striking cases of zygomorphy in this family, where actinomorphy characterizes the flowers of nearly all species, is emphasized.

Both *Streptanthus cutleri* and *S. carinatus* have greatly elongated racemose inflorescences on which it is usual for a single flower to mature at a time. There are successively maturing flowers from base to apex of the inflorescence. These are usually spaced about 2 cm. apart at the time of full anthesis. In each flower, the anthers mature before the stigma and, as shown in figs. 1-4, the stamens project slightly. At the same time, they occupy the area at the center of the flower and effectively cover the stigma which remains unexpanded and situated toward the base of the flower until well after the pollen has been shed. At the stage of anther maturity, the outer floral parts tightly close the flower entrance. Following anther maturation and the shedding of pollen, the ovary elongates, the stigma expands and the floral parts move to an open stance. The stigma becomes much enlarged and is brought by the elongating ovary and style to a central position below the entrance of the flower. The primary flow of nectar from the nectaries located at the base of the filaments and near the point of insertion of the petals coincides with stigma maturation rather than anther maturity. This is significant not only because it correlates with the opportunity of flower entry by insects and the receptivity of the stigma to pollen but because it actually avoids the time of anther maturation as well. The question as to what it is about the flowers in the closed condition, where nectar is not available, that attracts appropriate insects for pollen pick-up, is a pertinent one. We do not have a definite answer but we did notice that flower odor seemed to be at its peak during the period of anther maturity and pollen shedding. Odor, together with flower shape and perhaps color, may fulfill the requirements for insect attraction. On the other hand, it may be that the insects pollinating these flowers do not distinguish between the open and closed condition. If so, they would move from flower to flower indiscriminately, sometimes being rewarded by available nectar and sometimes not. In any case, the timing of pollen pick-up by the insect is effectively separated from pollen deposit not only by protandry but by several correlated reinforcing mechanisms in addition. The situation is approximately the same in *Streptanthus cutleri* and *S. carinatus*, although the flower form in these two species is radically different because of the differences in petal development. The petal color is also different. The petals of *S. cutleri* are light to reddish purple while those of *S. carinatus* are brownish white with the veins prominently purple. In both species the calyx is a deep blackish purple. Undoubtedly different insects pollinate these two species of *Streptanthus*. However, we have not observed insect visitation to the flowers of either species in its native habitat. Both species occur wholly in extreme western Texas.

Two levels of zygomorphy are shown by *Streptanthus carinatus* and *S. cutleri.* In the former, the stamen whorls



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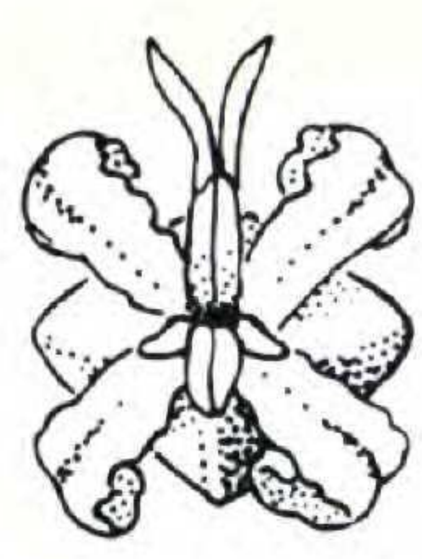

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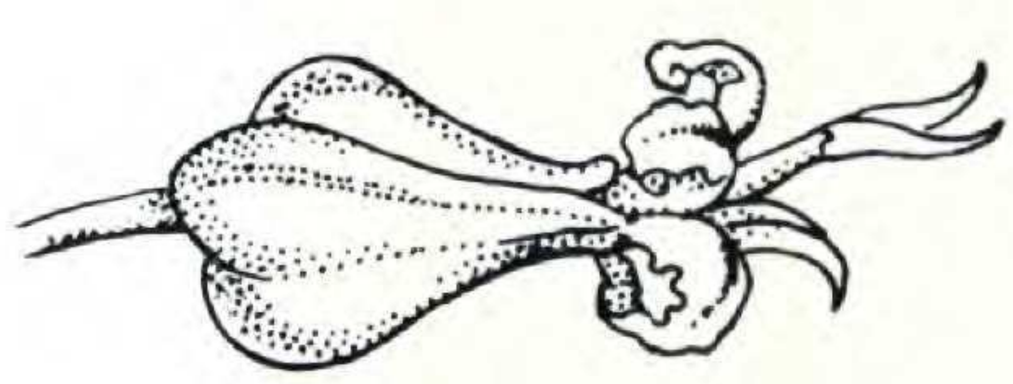

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Figs. 1-4. Flowers of *Streptanthus*, × 2. Fig. 1 & 2, face and side view respectively of *S. cutleri.* Fig. 3 & 4, face and side view respectively of *S. carinatus.* Drawings by Dorothy H. Marsh.

are strongly zygomorphic but the other floral parts show little or no zygomorphy. The situation is readily seen by reference to fig. 3 and 4. The filaments of the paired stamens, above and below, are of different lengths and the usual radial symmetry of the androecium present in most crucifer flowers is thereby considerably changed. A further change is seen in the tendency of the two single stamens to become associated with the lower paired stamens into a grouping of four with the anthers at about the same level of exsertion from the flower. Recurved petals further emphasize the prominence of the anther position. The androecium of *S. cutleri* is quite similar to that of *S. carinatus*, but the upper stamen pair is less exserted and the tendency of the single stamens "to platform" with the lower paired stamens is perhaps more strongly developed.

A strong zygomorphy is present in the corollas of *Streptanthus cutleri*. Here, the blades of the two lower petals have virtually been lost and the two upper bladed petals have become strictly upright. There is some variability between different plants as to the amount of blade present on the lower petals. This ranges from no blade at all, as shown in fig. 1 and 2, to a distinct asymmetrical blade of considerably smaller size than that present on the upper petals. The calyx also shows a noticeable but not highly developed zygomorphy in this species. The lower sepal is more pouched toward its base than any of the other three. This is shown in fig. 2.

In summary, it may be stated that *Streptanthus cutleri* and *S. carinatus* are protandrous and self-incompatible. These phenomena promote out-crossing between different plants of a given population. Protandry and self-incompatibility reinforce each other and thereby probably produce a nearly foolproof system of out-crossing. Several facets of flower behavior strengthen the separation of pollen pick-up and pollen deposit in a particular flower provided by the maturation sequence characteristic of protandry. These are (1) flower closure, preventing insect penetration and consequent self-pollination during anther dehiscence, (2) flower opening during the period of stigma receptivity, (3) nectar flow timed to coincide with stigma maturation and flower opening. — GRAY HERBARIUM, HARVARD UNIVERSITY.